

Memory Encoding of Object Relocation in a Hierarchical Associative Network with Theta Phase Coding

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Abstract- Memory of the natural environment corresponds to the complex alignments of objects and changes in their locations. We hypothesized that the neural dynamics of theta phase precession observed in the rat hippocampus should contribute to the memory of object-place associations because of its high selectivity in synaptic plasticity of an on-line process. Our computer experiments have demonstrated that object-place associations can be instantaneously stored in the hippocampus as a hierarchical associative network, where object-relocation is stored by rewiring its part in the network. It indicates an advantage of theta phase coding in the memory of the natural environment.

I. INTRODUCTION

Environments can be classified into objects and other larger entities. The objects can be relocated from time to time to provide changes in the environments. For example, a car's parking place can change every morning, and must be recalled in the evening. This type of memory, including both spatial and episodic contents, is known to critically depend on the medial temporal lobe, which consists of the hippocampus and parahippocampal regions [1].

According to anatomical knowledge, the hippocampus receives convergent inputs of "object" and "space" information through parahippocampal regions [2]. The hippocampus is known to be responsible for object-place associations under complexity in the memory contents and the instantaneous property [3, 4]. A number of theoretical studies have been devoted to hippocampal memory for fixed object-place associations [5, 6]. Until now, however, there has been no agreement on the neural mechanism that updates the memory of object-place associations.

A new neural mechanism of memory encoding in a one-time experience was recently proposed based on theta phase precession [7, 8], which was observed in the rat hippocampus [9, 10, 11]. In this theory, the behavioral

sequence (in a time scale of several seconds) is compressed by theta phase precession into a phase-specific firing sequence in every theta oscillation period (4 Hz - 12 Hz). Asymmetric synapses are selectively generated according to the synaptic plasticity asymmetric time window. This theory is different from other theories that require repeat learning [12]. Sato and Yamaguchi reported that theta phase coding enables robust memory to encode a temporal sequence in a one-time experience, instead of traditional rate coding [13]. Hesselmo et al. demonstrated that the dynamics of theta phase precession also enables goal directed rat navigation [14].

Recently theta phase coding was applied to a typical hippocampal dependent memory in humans, object-place associative memory [15]. It was demonstrated that the visual input sequence could be generated by a series of saccadic eye movements. This results in the instantaneous formation of a network for object-place associations. In this network, place-place associations are symmetric and distinguished from unidirectional connections for place-object associations. Thus, symmetry and asymmetry characterize one layer for places and another layer for objects, leading to a hierarchical structure of the network.

In this study, we elucidate whether or not theta phase coding can contribute to instantaneous change in object-place association memory during object relocations by rewiring the hierarchical associative memory network. However, it is a question of whether or not memory renewal could succeed without interference with another old memory even by one-time experience. Elucidation using computational experiments is given below.

II. NEURAL NETWORK MODEL

A. Basic Structures

Temporal sequences of retinal images are assumed to activate the hippocampus through visual pathways during an encoding period. According to anatomical evidence [2] and fMRI studies [16], we assume two visual information pathways. One processes the object in the central visual

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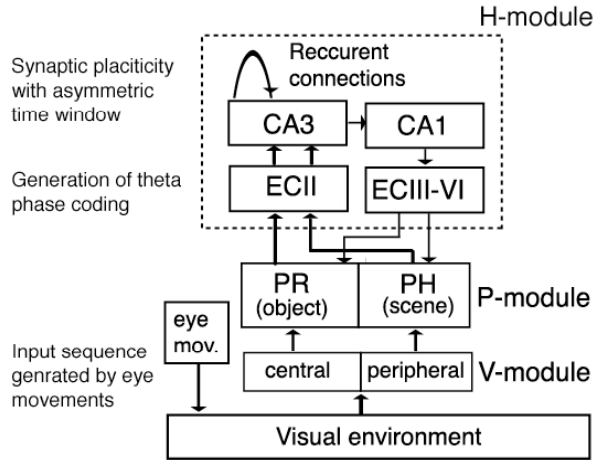


Fig. 1. Basic structure of the network model.

field and the other processes an entire image as a scene in the peripheral visual field.

The network consists of a visual environment, the V-module, the P-module, and the H-module, as illustrated in Fig. 1. This network was partially reported in a previous paper.

B. The Visual Environment

Visual environment is given by a number of objects with different colors and backgrounds with gray scale patterns. Every saccadic eye movement is assumed to catch an object in the central visual field. Subsequent retinal images around an eye movement overlap each other in the peripheral visual fields.

C. The V-Module (Visual System)

The V-module receives retinal image inputs from the visual environment and has color information in the central visual field and gray-scales in the peripheral visual field.

D. The P-Module (Parahippocampal Regions)

The P-module consists of the PR and PH layers, corresponding to the perirhinal and parahippocampal cortices, respectively. The PR layer receives an object input as color in the central visual field, and the PH layer receives a scene input of the peripheral visual field and processes a global feature of the retinal image.

E. The H-Module (Hippocampus)

The H-module is the network that associates object and scene inputs with theta phase coding. It consists of the ECII, CA3, CA1, and ECIII-VI layers, corresponding to the anatomical structure of the hippocampus [7, 8]. ECII receives the temporal sequences of object and scene inputs according to the saccadic eye movement series, and then

encodes them in the theta phase. In the CA3 layer, an associative memory is formed in recurrent connections based on the asymmetric time window of synaptic plasticity. A reactivation of the memory in the CA3 is projected into the PR and PH layers through the CA1 and ECIII-VI.

III. ANALYSIS

The visual environment in this study consists of two objects with different colors and a background having a gradual change in gray-scales (Fig. 2). The left object (object 2) is relocated to the right side of the other object (object 1). Three retinal images, 1, 2, and 2', are then introduced to the network. They overlap each other in the peripheral visual fields.

The computer experiment in this study was conducted in two stages, the encoding stage and recall stage. In the encoding stage, a given sequence of retinal images 1 and 2 generated by eye saccadic movements was introduced into the network. After that, the experiment shifted to the recall stage. During the recall stage, a retinal image was introduced into the V-module, and was examined to determine if the input sequence of the visual environment was generated in the CA3.

An additional encoding stage was introduced for object relocation. A sequence of retinal images 2 and 2' was introduced into the network. Again, the memory was evaluated in the recall stage.

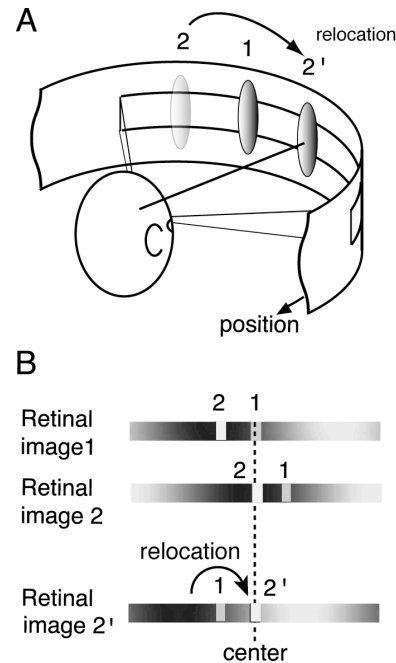


Fig. 2. (A) Visual environment that consists of two objects with different colors and a background with gray-scales. After encoding two object-scene associations, the object 2 is relocated to position 2'. (B) Retinal images that catch one object in the central visual field.

A. Connection Matrices before and after Object Relocation

The temporal evolution of units in the encoding stage is shown in Fig. 3. It is seen that the activation of units in the PH layer changes with overlaps among subsequent retinal images. In the CA3 layer, the theta phase to each activation of unit relative to theta rhythm gradually advances cycle by cycle. The phase difference among these units reflects the difference in the onset time of the input from the P-module. The relative phase between units encodes the “earlier-later” relation of the input’s onset time.

Connection matrices before and after the object relocation are displayed in Fig. 4. An equivalent graph of the network before object relocation shows that the unidirectional connections from scene to object units are formed. It is considered that the asymmetric connections are derived from theta phase coding where the temporal development of scene input is slower than the object inputs [15].

An equivalent graph of the network after object relocation shows the additional asymmetric connections. These are unidirectional connections from scene 2 to scene 2', from scene 1 to scene 2', and from object 1 to scene 2'. It is believed that the asymmetric connections among the scene units are caused by an input sequence similar to a sequence of rat place fields [8]. The unidirectional connection from object to scene units is another component.

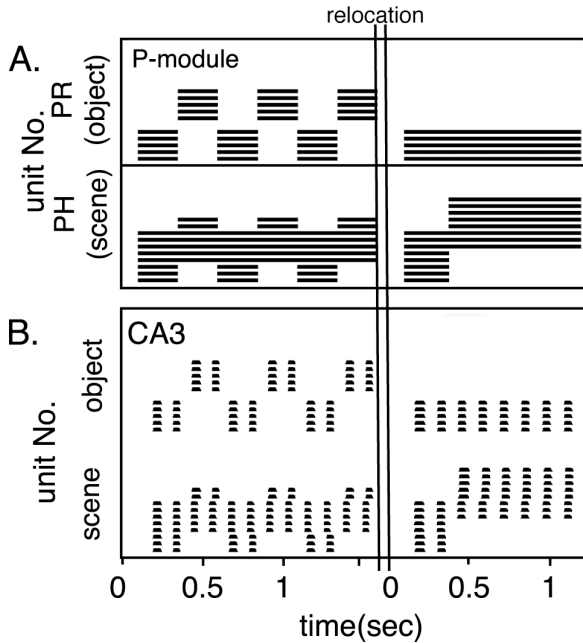


Fig. 3. Temporal evolution of the units. (A) Activation in the P-module. The abscissa and ordinate represent the time and unit number, respectively. Because of the overlap between successive retinal images in the peripheral visual fields, the activation in the PH layer appears gradually. (B) Phase precession pattern in the CA3 layer.

B. Memory Reactivations before and after Object Relocation

The memory is evaluated in the recall stage. Fig. 5 shows reactivations in the CA3 layer and in the P-module, where different cue inputs are introduced to the V-module as the initial activation. The reactivation in the CA3 layer shows that the individual sets appear sequentially one by one, and the reactivations of the network before object relocation show the object-scene associations before object relocation.

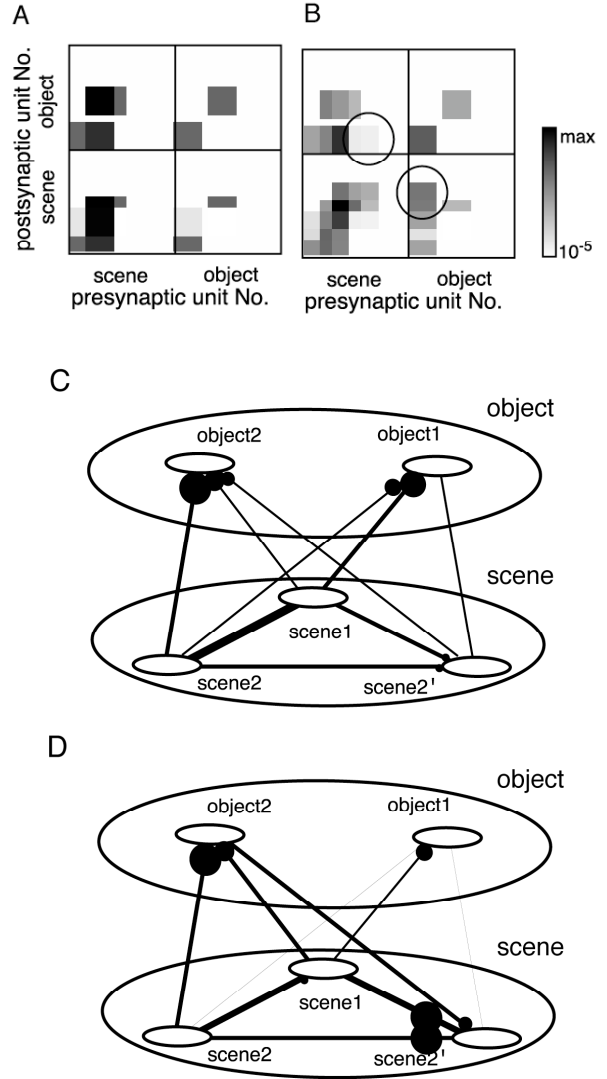


Fig. 4. Results of connection matrices in the CA3 layer. (A, B) Connection matrices before and after object relocation. The abscissa and ordinate represent the pre- and post-synaptic unit numbers, respectively. The gray level denotes the connection weight (the darker, the stronger). (C, D) Equivalent graphs. The nodes represent objects 1 and 2 and scenes 1, 2, and 2'. The thickness of the arrow indicates the strength of the connection and the size of the arrowhead represents the connection directionality. The connection matrix after object relocation additionally includes the unidirectional connections from scene 2 to scene 2', scene 1 to scene 2, and object 1 to scene 2'.

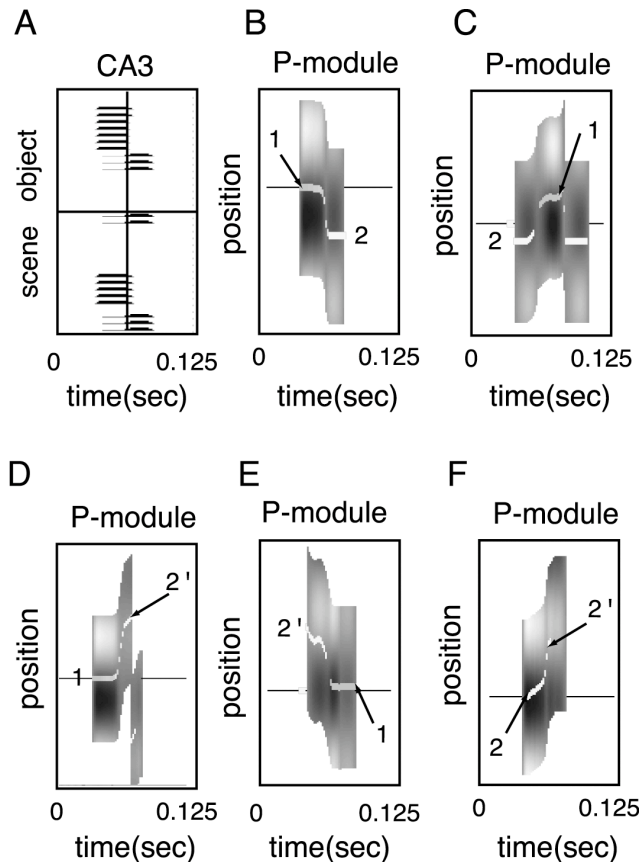


Fig. 5. Results of the recalled sequence in the same network. (A) Reactivation in the CA3 layer before object relocation. Initial activation of retinal image 1 is introduced to the V-module. The abscissa and ordinate represent the time and the unit number, respectively. (B, C) Reactivation of the P-module before object relocation. Initial activations of retinal image 1 and object 2 are introduced respectively. The object-scene associations are recalled one by one. (D, E, F) Reactivations of the P-module after object relocation. Initial activations of retinal image 1, object 2, and scene 2 are introduced respectively. In the first and second cases, new object-scene associations appear one by one. In the last case, a sequence of old-new associations for object 2 appears.

As explained in the previous section, the connection matrix after object relocation includes both old and new associations. The initial activation with a cue of object 2 successfully causes the reactivation of new object-place associations. In the same network, an initial activation with a cue of scene 2' (without object) generates a temporal sequence of old and new associations for object 2. This is the temporal sequence of object relocation. These results indicate that the reactivations in the network after object relocation are specific to initial cues, and these correspond with the environment.

C. Influence of Input Sequence for Object Relocation

In the above results, it is expected that the input sequence from old to new associations is essential for memory reformation. To investigate the importance of the

temporal sequence, a new object-scene association is encoded without successive activation as an event of object relocation. In this case, the connection matrix does not include asymmetry between old and new scenes, and the reactivation of old object-scene association appears without new association. This indicates that the asymmetric connection can be important in reforming memory.

V. DISCUSSIONS AND CONCLUSIONS

Our computer experiments demonstrated that, under a local change in the environment, all objects stay still except for the relocated one, and that the relocating object is flexibly linked to a unit for a new place in the hierarchical network. The memory encoding of object relocation causes the unidirectional connections from object to scene inputs in the hierarchical network. This indicates a mechanism and function of asymmetric connections discussed below.

Fig. 6 schematically illustrates asymmetric connections in the connection matrices, before and after object relocation. Before object relocation, theta phase coding of the input sequence forms unidirectional connections from scene to object units (see, Fig. 6A). An earlier onset of the scene units than object units is produced by overlaps among the subsequent retinal images. It is essential to form such asymmetric connections [15].

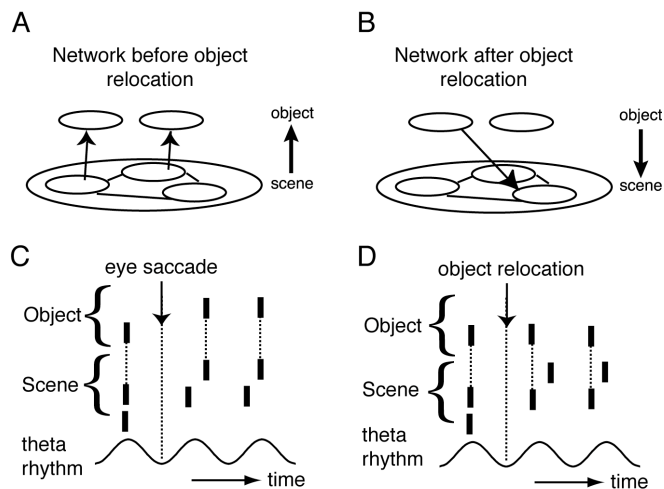


Fig. 6. Memories formed in the network before and after object relocation. (A) Theta phase coding of the retinal images produces a hierarchical structure of the network between object and scene inputs, where its direction is from scene to object units. (B) Theta phase coding of the input sequence for object relocations additionally produces the asymmetric structure of the network, where the direction is from object to scene inputs. Both asymmetric structures contribute to the reactivation of object-place association memory. (C) An earlier onset of scene units than object units is produced by overlaps of subsequent retinal images. It makes an earlier phase of scene unit to object unit that results in a unidirectional connection from scene to object units, according to STDP. (D) The object relocation causes an earlier onset of object units than scene units. It results in a unidirectional connection from object to scene units.

By contrast, after object relocation, unidirectional connections are additionally formed from object to scene units (see, Fig. 6B). The unidirectional connection direction is opposite the case before object relocation. The reason is believed to be the encoding of an object relocation instance that causes an earlier onset of object units than new scene units. This results in a formation of unidirectional connections from object to scene units. It is considered that these unidirectional connections can appear transiently, and its direction changes in a subsequent encoding of new associations.

Both directions of unidirectional connections can work simultaneously, as shown in Section IV-C. Roles of unidirectional connections from scene to object units, and from object to scene units, are considered to store a stable environment and a transient event, respectively.

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